Biogeochemistry (2012) 109:1–6
DOI 10.1007/s10533-011-9614-y

The role of environmental microorganisms in ecosystem responses to global change: current state of research and future outlooks

Kathryn M. Docherty · Jessica L. M. Gutknecht

Received: 2 June 2011 / Accepted: 4 June 2011 / Published online: 24 September 2011

The effects of human activities have dramatically altered our natural environment. Greenhouse gas production, nutrient loading, land-use change and water consumption, to name a few, can dramatically affect ecosystem processes by changing the dynamics of global biogeochemical cycles. Currently, one of the most crucial scientific objectives is to gain an understanding of how drastically anthropogenic changes have altered our planet and what those changes mean for the future.

In order to predict accurate scenarios of how global change will affect terrestrial ecosystems, the effects and controls over biogeochemical pools and fluxes, as incorporated into predictive global change models, must be carefully examined. This is not only necessary to guide scientific endeavor, but also to inform policymakers and to serve as a basis for advocacy of social change. By examining and understanding the dynamics of carbon, nitrogen, and other nutrient transformations scientists can take the pulse of an ecosystem and predict changes into the future. Many of these biogeochemical cycles are catalyzed by abundant and diverse microorganisms, the "gatekeepers" that populate every ecosphere. However, most global change models treat "microbes" as a single pool, responsible for a single rate of flux (Todd-Brown et al. 2011; Treseder et al. 2011).

Advances in microbial molecular techniques, and increasing integration between microbiological and ecological disciplines have provided overwhelming evidence that microbial communities are far more diverse than could ever have been imagined (e.g. Roesch et al. 2007; Fierer and Jackson 2006; Schloss and Handelsman 2006; Gans et al. 2005). With these insights comes a whole new body of evidence that microorganisms are not simple bags of enzymes, the abundance of which directly relate to the rate of a chemical reaction in the environment. On the contrary, we find that microorganisms are dynamic catalysts with a rich evolutionary history spread across all three domains of life. This life history shapes what metabolic capabilities microorganisms have, and how they respond to a diverse array of ecological constraints, including nutrient and dispersal limitation, competition, predation, cooperation and disturbance. Microorganisms themselves are affected by the global changes that occur, and shifts in microbial communities are inevitably linked, through the biogeochemical cycles they mediate, to the entire ecosystem. How

K. M. Docherty (✉)
Department of Biological Sciences, Western Michigan University, 1903 West Michigan Ave, Kalamazoo, MI 49008, USA
e-mail: kdochert8@gmail.com

K. M. Docherty
National Ecological Observatory Network (NEON, Inc.), 1685 38th St. Suite 100, Boulder, CO 80301, USA

J. L. M. Gutknecht
Department of Soil Ecology, Helmoltz-Centre for Environmental Research-UFZ, Theodor-Leiser-Strasse 4, 06120 Halle, Germany

microorganisms respond to global change, particularly those responsible for greenhouse gas production through processes such as decomposition, methanogenesis and denitrification, is integral information that must be incorporated into accurate global change models.

This special issue includes eight papers that emanated from an Ecological Society of America Special Symposium "Microbial gate-keepers and climate change: new insights relating microorganisms, global change and ecosystem processes" in August 2010. The issue includes a variety of manuscript types, including syntheses (e.g. Treseder et al. 2011; Dooley and Treseder 2011), theoretical idea papers (Wallenstein and Hall 2011; Todd-Brown et al. 2011), field observations (Yavitt et al. 2011) and manipulative experiments (Evans and Wallenstein 2011; Brown et al. 2011; Docherty et al. 2011). The common theme across all contributions is that microorganisms in the natural environment can either mediate or expedite the effects of anthropogenic global change. Understanding the regional and global roles of microbes is necessary to accurately predict the direction and magnitude of these effects.

Several common directions for future research that will enhance our understanding of microbial roles in global change have been suggested both in the special issue and during the panel discussion following the ESA session. These courses of action fall into two categories; 1) the inclusion of microbial dynamics in global change models and 2) the gathering of appropriate microbial data for the validation of those models.

The need for microbe-inclusive models and their validation

It is crucial, but rare, to validate the performance of microbe-inclusive global change models using empirical data, and to benchmark those models against conventional microbe-exclusive models (Treseder et al. 2011). Only one of the four case studies presented in Treseder et al. (2011) was validated with empirical data against a conventional model. This model suggests that explicit microbial terms related to extra-cellular enzyme production and bio-available carbon enhance predictability of soil respiration (and C cycling) under pulsed precipitation regimes (Lawrence et al. 2009). As presented in Todd-Brown et al. (2011), the latest IPCC (2007) report assumes that decomposition is a first-order decay process, proportional to the size of the carbon pool, not microbial biomass. However, they argue that climate predictions could be substantially improved by treating decomposition as a second-order process related to the size and enzyme activity of microbial communities (Todd-Brown et al. 2011). Wallenstein and Hall (2011) extend this idea to suggest that spatially explicit microbial adaptation may play an important role in how quickly microbial communities can respond to rapid global change. By treating different eco-regions (e.g., extreme temperature ranges versus narrow temperature ranges) according to their specific microbial adaptation rates, more accurate global change models can be created (Wallenstein and Hall 2011).

The need for informative empirical microbial data

In many cases, validation of microbe-inclusive global change models cannot be performed, simply because the appropriate data does not exist. The types of datasets, that are most informative for global change models fall into several categories including long-term microbial datasets, cross-biome datasets, and high-resolution, accurate, multi-factorial field datasets.

Long-term microbial datasets

It is unclear if short-term responses will apply to global change manipulations spanning decades during which microbial communities may adapt and evolve (Todd-Brown et al. 2011). For example, over the short-term, soil microbial respiration increases with elevated temperature (Treseder et al. 2011). However, long-term, this effect is reduced, and microbial respiration returns to ambient levels, despite the increase in temperature (Treseder et al. 2011). Presumably, over the longer-term, microbial growth and enzyme efficiencies could decline, enzymes could be down-regulated and more slowly respiring microbial taxa could become more dominant in the community (Treseder et al. 2011).

The three papers included in this special issue that include multi-year datasets indicate the need for longer-term datasets as well. Inter-annual variation and interactions with changes in the plant community can substantially influence microbial responses to

manipulative global change treatments (Docherty et al. 2011; Evans and Wallenstein 2011; Brown et al. 2011). In many cases, a global change treatment may affect microbial biomass or activity in one year of a study, but only consistent responses can be interpreted as long-term effects that can inform a predictive model (e.g. Docherty et al. 2011; Evans and Wallenstein 2011; Brown et al. 2011).

Cross-biome datasets

In addition to long-term, consistently collected datasets, there is a substantial need to determine differences in microbial responses to global change by specific biome or ecosystem. For example, Dooley and Treseder (2011) performed a meta-analysis of the effects of fire in several different biomes. Shifts in microbial biomass, fungal:bacterial ratios and the microbial recovery time following a fire can vary dramatically depending on whether the fire occurs in temperate grasslands, boreal forests, temperate forests, or shrublands (Dooley and Treseder 2011). Yavitt et al. (2011) examined peatlands across a 775 km gradient in the Appalachian Mountain region, and found that geographic distance, site history, and local climate play key roles in determining what specific functional groups of methanogenic archaea are present. Evans and Wallenstein (2011) found that soils subjected to a climate history of altered rainfall regimes responded differently to new changes in soil wetting regimes than soils from biomes with regular precipitation patterns.

Given these differences between biomes and the influence of local climate history, traditional coupled global change models that operate within a spatial resolution of about $1 \times 1^{\circ}$ in area will fall short, because they will include high levels of microbial diversity and potentially several different biome types (Todd-Brown et al. 2011). If, as Wallenstein and Hall (2011) suggest, historical temperature and precipitation regimes play a role in how quickly microbial communities can adapt to rapid environmental shifts, then incorporating regional microbial aspects into global change models will be necessary for accurate global predictions. Wallenstein and Hall (2011) argue that ecosystems containing more extensive aquatic components will have a relatively lower amount of annual fluctuation in temperature than geographically adjacent arid regions. Combining terrestrial data with data collected from riparian zone and aquatic systems such as wetlands, lakes and streams, especially those impacted by land-use change and agricultural run-off, will provide a more complete picture of within-region variability.

High-resolution, accurate, and multi-factorial field data

Todd-Brown et al. (2011) suggest a model framework based on microbial enzyme kinetics, where decomposition is related to the amount and diversity of microbial enzymes in relation to the amount and diversity of carbon sources. In order to validate such a model, specific estimates of microbial enzymatic reactions must be provided, over the long-term and across several biomes. However, most enzyme measurements cannot be done under field conditions, but must be done in the laboratory, where enzyme rates might be altered (Todd-Brown et al. 2011). The development of techniques that predict function based on microbial data that can be collected in the field, such as RNA-based metagenomics and proteomics, could aid in predicting what microbial functions are present at a specific site. However, this cannot replace an accurate rate of enzyme activity or other functional measurements in the field. An even greater challenge is that even under field conditions, there is very little knowledge about the persistence versus turnover of extra-cellular enzymes. This presents a challenge to linking measured activities with the physiology, metabolism, or composition of the microbial community. Development and expansion of methods to accurately assess microbial characteristics, activities and properties in soils is essential for advancing use of microbial mechanisms in ecosystem models (Treseder et al. 2011).

While limited by the techniques that are available, future research that relies on in situ sensors of microbial processes, such as automated chamber systems, pooled-dilution stable isotope experiments or minirhizotrons, are preferable over measurements of potential rates under ideal conditions, or net rates in fluctuating field conditions (Treseder et al. 2011; Wallenstein and Hall 2011). Additionally, coupling field-level experiments with specific laboratory experiments can aid in teasing apart the effects of a particular treatment on the microbial community component of an ecosystem response. For example,

Evans and Wallenstein (2011) found that when soils had been exposed to altered long-term field-level rainfall regimes, the historical impact of drought resistance still remained in the microbial community when soils were used in a mesocosm experiment that further varied the soil moisture regimes without the indirect plant community and other environmental factors involved.

When laboratory experiments are not possible, multi-factorial field experiments are useful in determining microbial responses to multiple global change factors. The Jasper Ridge Global Change Experiment, which simultaneously manipulates four treatments, is used in two papers in this special issue to examine field-level effects of global change to soil microbial communities. Docherty et al. (2011) found that increased soil ammonium concentrations as a result of a nitrogen deposition treatment yielded a substantial increase in ammonia-oxidizing bacterial abundance. However, when similar soil ammonium concentrations were achieved through burning of above-ground biomass, ammonia-oxidizing bacterial abundance did not increase, suggesting a complex relationship between microbial and plant communities that can be influenced by global change. Brown et al. (2011) show that multiple global change factors can affect N_2O production, and that both denitrification and nitrification contribute its production. Both these papers indicate that it is just as important to examine the microbial drivers and mechanisms behind a biogeochemical process as to examine the process itself.

Ultimately, all microbial data are limited by similar technological constraints, and accurately informing global change models in the future will require addressing these constraints. All DNA-based techniques are limited by extraction biases which depend on soil type and the ratio of target DNA (or RNA) to chemical inhibitors. While purified DNA or cDNA alone can be used for certain techniques, such as metagenomics, most microbial community analyses rely on amplification by PCR. PCR is also limited by probe biases, the identification of informative gene regions, the number of base pairs in a gene that it is possible to sequence to obtain meaningful phylogenetic information, as well as sufficient reference sequences to build an accurate reference alignment and phylogenetic tree. PCR-based techniques have provided the majority of microbial information thus far, but is often based on genes that can only be resolved to a family level (such as the methanogens described in Yavitt et al. 2011 and the ammonia-oxidizers described in Docherty et al. 2011).

Little information exists about how different sub-groups of microorganisms may be responsible for different rates of biogeochemical reactions, or how they adapt to shifts in environmental factors. Docherty et al. (2011) indicate that the cluster 3a sub-group of ammonia-oxidizers responds to nitrogen deposition, suggesting that particular clades within a phylogeny may have different life histories, and different metabolic capabilities than their neighbors who contain the same functional gene. Similarly, Yavitt et al. (2011) found that only one type of methanogen was ubiquitous across all six of their geographically distant peatlands, but that the majority of methanogens identified were unique to each site. However, assessing how particular clades of ammonia-oxidizers, or how ubiquitous versus site-specific methanogens, are related to nutrient cycling rates can currently only be done using pure cultures of these microorganisms, which are difficult or impossible to obtain.

While further work on specific within-microbial community controls on biogeochemical cycling is necessary, very little information is known about the external biotic controls of microbial communities through food web and trophic interactions. For instance, the role of top–down controllers such as eukaryotic microbial predators (e.g., nematodes) or bacteriophage on soil microbial communities is poorly understood, and how these roles will shift in the face global changes is largely unknown.

Outlooks

Despite the many challenges involved with incorporating microbial data into global change models, and the validation of those models, there are many promising modeling efforts and methods which begin to address these challenges. Recent modeling efforts incorporating microbial dynamics include microbial C dynamics with global warming (Allison et al. 2010), microbial physiology and altered soil moisture regimes (Lawrence et al. 2009), microbial feedbacks to N deposition and C cycling (Gerber et al. 2010), and several models to address microbial controls on decomposition (Todd-Brown et al. 2011). In addition to providing a theoretical framework, these efforts also

serve to synthesize current knowledge and pinpoint the datasets most needed for more predictive future microbial knowledge in the face of global change (for a full description of these modeling efforts see Treseder et al. 2011 and Todd-Brown et al. 2011).

Recently-developed techniques have started to approach obtaining a high-resolution, accurate level of microbial information, which would ultimately be extremely useful for predicting the role of specific microbial communities in global change models. Several of these techniques were described by Treseder et al. (2011) and include: nucleotide analog labeling and stable isotope probing which both reveal the active microbial community; NanoSIMS and fluorescence in situ hybridization which can link the active, labeled community with environmental function; RNA analysis can also determine the actively functioning community; and ^{13}C phospholipids fatty acid analysis which can be used to trace carbon through broad microbial groups. There are also new research efforts to better determine accurate in situ enzyme activity (Wallenstein and Weintraub 2008) and to better understand how enzyme activities fluctuate over time (Bell and Henry 2011). In addition, techniques such as functional genetics can be paired with proteomics and metabalomics in order to link phylogeny with physiology and measurements of environmental function. The pairing of techniques can also serve to validate the value of each method independently. Currently, most of these methods require sophisticated equipment and are relatively expensive. Through further development, these methods will be able to be used in a broader scale to encompass multiple year or multiple biome studies.

As the technology develops, the need for the combination of long-term and cross-biome microbial data can be informed, in part, by datasets collected by organizations such as the National Ecological Observatory Network (NEON), the Long-Term Environmental Research, and the Long-term Research in Environmental Biology (LTREB) program. These efforts to provide long-term continuous field sites make it feasible for researchers in the scientific community to install additional equipment to test and measure in situ activity rates such as soil respiration (soil collars), trace gases (soil septa), nutrient flow (lysimeters) or root/hyphae growth (minirhizotrons) over the long-term. These programs also serve as an excellent testing ground new sensor techniques which can be compared against historical or simultaneous data already collected at the sites using traditional methods. Additionally, within the infrastructure of these programs, the long-term and cross-biome microbial datasets collected provide a general background of continental-scale microbial data. This can directly inform and foster further empirical research in the scientific community that can be used to address specific microbial parameters in global change models. To utilize these new tools, techniques, field sites and databases to their greatest capacity, it is most crucial for empirical and theoretical investigators to collaborate closely in this emerging field of "global change microbial ecology". With long-term data that can sufficiently inform and validate particular regional and global change models with explicit microbial terms, we can begin to truly understand the extent of the role of microorganisms as biogeochemical catalysts in our environment.

Acknowledgments The guest editors would like to express their gratitude to the Microbial Ecology, Biogeosciences and Soil Sciences Sections of the Ecological Society of America for sponsoring the symposium that inspired this special issue. Additionally, the symposium would not have been possible without travel funding from the United States Department of Energy (DOE 00001781079218). We would specifically like to thank Joseph Graber (DOE) for his encouragement and help with obtaining this travel funding. We would like to thank the eight invited speakers who participated in this symposium and panel discussion and Jessica Gutknecht, (Helmholtz-Centre for Environmental Research-UFZ) who moderated the session: Steve Allison, UC-Irvine; Teri Balser, University of Wisconsin-Madison; Brendan Bohannan, University of Oregon; Hinsby Cadillo-Quiroz, University of Illinois, Urbana-Champaign; Kathryn Docherty, University of Oregon; Audrey Niboyet, Université de Lyon; Kathleen Treseder, UC-Irvine; Matt Wallenstein, Colorado State University. PDF and MP3 files of these talks can be accessed through Nature Precedings by searching the author name within the ESA 2010 archive at http://precedings.nature.com/collections/esa-2010. Finally, we would like to thank Kate Lajtha, Editor-in-Chief of Biogeochemistry for her interest in the publication of this special issue, Brighid Docherty for her artistic expertise on the cover design, and the nineteen external reviewers for their comments and suggestions for the manuscripts presented here.

References

Allison SD, Wallenstein MD, Bradford MA (2010) Soil-carbon response to warming dependent on microbial physiology. Nat Geosci 3:336–340

Bell TH, Henry HAL (2011) Fine scale variability in soil extracellular enzyme activity is insensitive to rain events

and temperature in a mesic system. Pedobiologia 54:141–146

Brown JR, Blankinship JC, Niboyet A, van Groenigen CJ, Dijkstra P, Leadley PW, Hungate BA (2011) Effects of multiple global change treatements on soil N_2O fluxes. Biogeochemistry. doi:10.1007/s10533-011-9655-2

Docherty KM, Balser TC, Bohannan BJM, Gutknecht JLM (2011) Soil microbial responses to fire and interacting global change factors in a California annual grassland. Biogeochemistry. doi:10.1007/s10533-011-9654-3

Dooley S, Treseder KK (2011) The effect of fire on microbial biomass: a meta-analysis of field studies. Biogeochemistry. doi:10.1007/s10533-011-9633-8

Evans SE, Wallenstein MD (2011) Soil microbial community response to drying and rewetting stress: Do microorganisms adapt to altered rainfall timing? Biogeochemistry. doi:10.1007/s10533-011-9638-3

Fierer N, Jackson RB (2006) The diversity and biogeography of soil bacterial communities. Proc Natl Acad Sci (USA) 103:626–631

Gans J, Wolinsky M, Dunbar J (2005) Computational improvements reveal great bacterial diversity and high metal toxicity in soil. Science 209:1387–1390

Gerber S, Hedin LO, Oppenheimer M, Pacala SW, Shevliakova E (2010) Nitrogen cycling and feedbacks in a global dynamic land model. Glob Biogeochem Cycles 24:1001

IPCC (2007) Working group I contribution to the IPCC fourth assessment report. Climate change 2007: the physical science basis

Lawrence CR, Neff JC, Schimel JP (2009) Does adding microbial mechanisms of decomposition improve soil organic matter models? A comparison of four models using data from a pulsed rewetting experiment. Soil Biol Biochem 41:1923–1934

Roesch LFW, Fulthorpe RR, Riva A, Casella G, Hadwin AKM, Kent AD, Daroub SH, Camargo FAO, Farmerie WG, Triplett EW (2007) Pyrosequencing enumerates and contrasts soil microbial diversity. ISME J 1:283–290

Schloss PD, Handelsman J (2006) Toward a census of bacteria in soil. PLOS Comput Biol 2:786–793

Todd-Brown K, Hopkins F, Kivlin S, Talbot J, Allison SD (2011) A framework for representing microbial decomposition in coupled climate models. Biogeochemistry. doi:10.1007/s10533-011-9635-6

Treseder KK, Balser TC, Bradford MA, Brodie EL, Dubinsky EA, Eviner VT, Hofmockel KS, Lennon JT, MacGregor BJ, Pett-Ridge J, Waldrop MP (2011) Integrating microbial ecology into ecosystem models: challenges and priorities. Biogeochemistry. doi:10.1007/s10533-011-9636-5

Wallenstein MD, Hall EK (2011) A trait-based framework for predicting when and where microbial adaptation to climate change will affect ecosystem functioning. Biogeochemistry. doi:10.1007/s10533-011-9641-8

Wallenstein MD, Weintraub MN (2008) Emerging tools for measuring and modeling the in situ activity of soil extracellular enzymes. Soil Biol Biochem 40:2098–2106

Yavitt JB, Yashiro E, Cadillo-Quiroz H, Zinder SH (2011) Methanogen diversity and community composition in peatlands of the central to northern Appalachian Mountain Region, North America. Biogeochemistry. doi:10.1007/s10533-011-9644-5